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THE SYSTEMATIC STATUS OF
PEROGNATHUS MERRIAMI ALLEN

By Don E. Wilson
*Bird and Mammal Laboratories, National Museum
of Natural History, Washington, D.C. 20560*

In 1892, J. A. Allen named *Perognathus merriami* on the basis of 17 silky pocket mice from the vicinity of Brownsville, Texas. He compared this material with specimens of *P. flavus* from El Paso and concluded that they represented distinct species. He also figured six skulls of *P. merriami* and three of *P. flavus.*

Allen used the following characters to distinguish *P. merriami* from *P. flavus*: ". . . brighter and more yellowish in coloration, the sides being strongly yellowish or golden instead of pale cinnamon. . . . generally brighter yellowish color, particularly along the sides. . . . the skull is much larger and disproportionately broader in proportion to the length. The mastoids are shorter and less developed, leaving a much broader intermastoid area, with the interparietal much broader than long, instead of nearly square as in *P. flavus.*"

W. H. Osgood (1900), in his revision of the genus *Perognathus*, named *Perognathus merriami gilvus* based on three specimens from west Texas and four from Eddy (= Carlsbad), New Mexico. Osgood recognized the difficulty of separating his specimens from *P. flavus*: "This subspecies combines to some extent the characters of *flavus* and *merriami.*"

I have studied more than 250 specimens of *P. merriami* and *P. flavus*, including the types of *P. merriami*, *P. merriami gilvus*, *P. flavus bimaculatus*, *P. f. fuliginosus*, *P. f. hopiensis*, *P. f. mexicanus*, *P. f. piperi*, and *P. f. sonoriensis*. I report here the results of a discriminant function analysis which leads me to believe that *P. merriami* and *P. flavus* are conspecific.

Fɪɢ. 1. Map showing collecting localities of *Perognathus merriami* ■, *Perognathus flavus* ●, and *Perognathus merriami gilvus* ▲. ⊛ indicates locality of supposed sympatry of *P. flavus* and *P. m. gilvus.*

Methods

Figure 1 shows the specimen localities listed in Table 1. All specimens are study skins, skulls, or both. A total of 24 characters was used in the discriminant function analysis;

TABLE 1.   Samples of *Perognathus* examined

Sample Locality	Used in Multivariate Analysis	Additional
Perognathus merriami gilvus		
Mexico, Coahuila, 15SE Langtry, Texas	1	1
New Mexico, Carlsbad	5	
New Mexico, Roswell, 40W		1
New Mexico, Tucumcari, 25W	1	1
Texas, Presidio Co.	1	
Texas, Langtry	4	4
Texas, Comstock	3	
Texas, Stanton	1	
Texas, Washburn	2	
Texas, Big Springs	1	
Texas, Fort Lancaster	4	3
Texas, Marathon, 15S		1
Texas, Marathon		1
Texas, Boquillas	1	2
Texas, Juno, 20E	1	
Texas, Rock Spring		1
Texas, Japonica, 15W		1
Texas, Howard, 5S	1	
Texas, Monahans	3	3
Texas, Comstock, 10S	1	
Texas, Van Horn	1	
Texas, Samuels	1	1
Texas, Eagle Pass		1
Texas, Mobeetie	1	1
Texas, Kermit, E	8	1
Texas, Magic City, 1N	1	
Subtotals	42	23
Perognathus merriami merriami		
Mexico, Coahuila, Monclova	2	
Mexico, Coahuila, Sabinas		3
Mexico, Coahuila, Saltillo		1
Mexico, Nuevo Leon, Linares	1	
Mexico, Nuevo Leon, Doctor Cos	1	
Mexico, Nuevo Leon, Aldama		2
Mexico, Tamaulipas, C. Victoria	4	5
Mexico, Tamaulipas, Hidalgo	5	2
Mexico, Tamaulipas, Mier	3	2
Mexico, Tamaulipas, Matamoros, 10S	2	
Mexico, Tamaulipas, Reynosa		3
Mexico, Tamaulipas, Alta Mira		1

TABLE 1.   (Continued)

Sample Locality	Used in Multivariate Analysis	Additional
Mexico, Tamaulipas, Nuevo Laredo	2	3
Mexico, Tamaulipas, Camargo	1	2
Mexico, Tamaulipas, Soto La Marina	2	
Texas, Brownsville	29	2
Texas, Blocker Rancho		1
Texas, Rio Grande City		1
Texas, Padre Island	1	2
Texas, Santa Rosa	4	6
Texas, Kerrville		3
Texas, Brownsville, 20E		1
Texas, Mason		1
Subtotals	57	41
Perognathus flavus flavus		
Mexico, Chihuahua, Gallego		1
Mexico, Chihuahua, Chihuahua	2	8
Mexico, Chihuahua, Escalon	1	1
New Mexico, Deming		2
New Mexico, Chico Springs		1
New Mexico, Dog Spring		1
New Mexico, Carrizozo	4	
New Mexico, Tularosa	4	1
New Mexico, Santa Rosa	6	1
New Mexico, Ribera		1
New Mexico, Mesa Jumanes	1	
New Mexico, Manzano Mtns.	3	3
New Mexico, Grants	3	
New Mexico, Carlsbad	1	1
New Mexico, Rio Puerco		1
New Mexico, Quemado, 10SW	1	
New Mexico, Glenwood	1	
New Mexico, Laguna		2
New Mexico, Hachita		1
New Mexico, Playas Valley	1	
New Mexico, Gila National Forest, Diamond Creek	1	
New Mexico, Fairview		1
New Mexico, Reserve, 5NE		1
New Mexico, Vaughn, 5W	1	1
Texas, El Paso	1	4
Texas, Sierra Blanca		1
Texas, Valentine	1	
Texas, Alpine		1
Subtotals	32	34

TABLE 1.   (Continued)

Sample Location	Used in Multivariate Analysis	Additional
Perognathus flavus medius		
Mexico, San Luis Potosi, Hacienda La Parada	1	2
Mexico, San Luis Potosi, Jesus Maria	1	2
Perognathus flavus bunkeri		
Colorado, Loveland	1	8
Perognathus flavus hopiensis (type)		
Arizona, Oraibi	1	
Perognathus flavus mexicanus (type)		
Mexico, Distrito Federal, Tlalpam		1
Perognathus flavus piperi (type)		
Wyoming, Newcastle	1	
Perognathus flavus sonoriensis (type)		
Mexico, Sonora, Costa Rica Ranch		1
Perognathus flavus fuliginosus (type)		
Arizona, San Francisco Mtn.		1
Perognathus flavus bimaculatis (type)		
Arizona, Fort Whipple		1
Subtotals	5	16
Totals	136	114

nine were skull characters measured to the nearest .05 mm with dial calipers, eight were skin measurements or scores, and seven were ratios (Table 2). The characters used were as follows:

Occipitonasal length.—Medial distance from the tip of the nasals to the posteriormost margins of the condyles.

Frontonasal length.—Medial distance from the tip of the nasals to the frontoparietal suture.

Nasal length.—Medial distance from the tip of the nasals to the nasal–frontal suture.

Least interorbital constriction.—The least distance across the skull between the orbits.

Mastoid breadth.—Greatest width of the skull across the mastoid bones.

Bullar length.—Greatest length of the auditory bulla.

Interparietal length.—Greatest length of interparietal bone.

TABLE 2. Means and standard deviations of the 24 characters used in the discriminant function analysis

Character	P. merriami (n = 57)		P. m. gilvus (n = 42)		P. flavus (n = 37)	
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
1. Bullar length Occipitonasal length	0.354	0.010	0.359	0.012	0.388	0.017
2. Background color	4.193	0.766	3.214	0.813	2.568	0.835
3. Tail length Total length	0.490	0.029	0.488	0.026	0.452	0.035
4. Mastoid breadth	11.277	0.377	11.442	0.409	11.930	0.431
5. Nasal length	7.343	0.371	7.375	0.279	7.203	0.345
6. Frontonasal length	13.696	0.450	13.719	0.404	12.991	2.246
7. Postauricular patch	2.053	0.580	2.762	0.726	3.108	0.774
8. Lateral line	2.421	0.596	1.500	0.672	1.378	0.492
9. Interparietal width	3.532	0.368	3.323	0.390	3.053	0.267
10. Dorsal black	3.632	0.645	2.929	0.778	3.054	0.405
11. Interparietal length	2.469	0.226	2.486	0.242	2.555	0.209
12. Interparietal width Mastoid breadth	0.314	0.035	0.290	0.032	0.256	0.026

TABLE 2. (Continued)

| Character	P. merriami (n = 57)		P. m. gilbus (n = 42)		P. flavus (n = 37)	
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
13. Maxillary toothrow length	2.986	0.136	3.056	0.137	2.953	0.165
14. Hind foot length Total length	0.141	0.010	0.143	0.007	0.145	0.009
15. Silkiness	3.561	0.501	2.786	0.645	2.784	0.584
16. Bullar length	7.123	0.271	7.318	0.261	7.846	0.386
17. Occipitonasal length	20.141	0.632	20.401	0.578	20.245	0.704
18. Nasal length Occipitonasal length	0.364	0.011	0.362	0.010	0.356	0.010
19. Mastoid breadth Occipitonasal length	0.560	0.013	0.561	0.017	0.589	0.014
20. Least interorbital constriction	4.605	0.174	4.712	0.235	4.436	0.187
21. Total length	113.930	7.198	116.429	4.467	113.270	5.635
22. Hind foot length	16.070	0.961	16.667	0.786	16.351	0.857
23. Tail length	55.772	4.375	56.833	4.060	51.243	5.035
24. Maxillary toothrow length Occipitonasal length	0.148	0.007	0.150	0.006	0.146	0.007
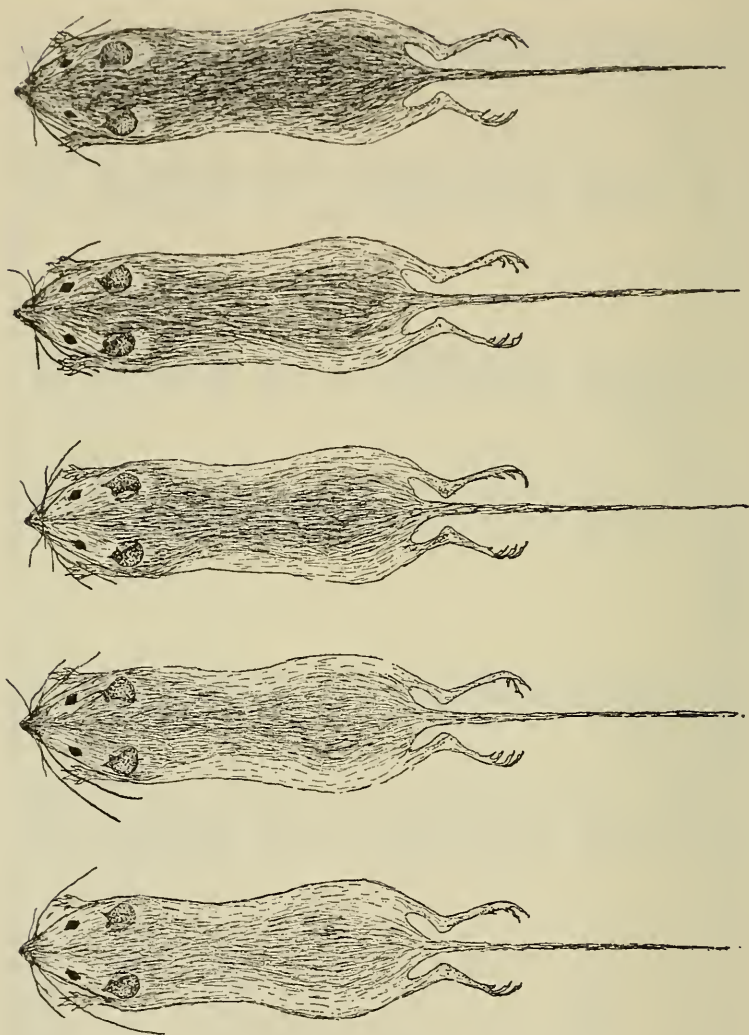
Fig. 2. Five standards used for scoring skins for amount of dorsal black and degree of development of postauricular patches.

Interparietal width.—Greatest width of interparietal bone.

Maxillary toothrow length.—Alveolar length of the upper cheek teeth.
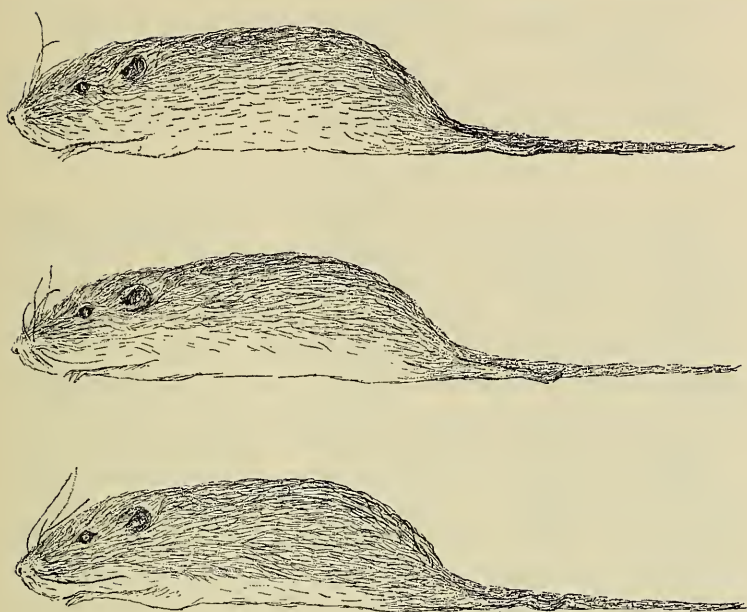
Nasal length/Occipitonasal length

Fig. 3. Three standards used for scoring skins for degree of development of lateral line.

Mastoid breadth/Occipitonasal length
Bullar length/Occipitonasal length
Interparietal width/Mastoid breadth
Maxillary toothrow length/Occipitonasal length
Total length.—Recorded from skin tags.
Tail length.—Recorded from skin tags.
Hind foot length.—Recorded from skin tags.
Tail length/Total length
Hind foot length/Total length
Background color.—Color of the dorsal underfur scored from 1 (light pinkish) to 5 (bright yellowish orange).
Amount of dorsal black.—Color of the dorsal guard hairs scored from 1 (light) to 5 (dark). See figure 2.
Postauricular patch.—Degree of development of postauricular patches scored from 1 (none) to 5 (large). See figure 2.

Silkiness.—Softness of the pelage scored from 2 (silky) to 4 (harsh).

Lateral line.—Degree of development of lateral line scored from 1 (indistinct) to 3 (distinct). See figure 3.

STATISTICAL TECHNIQUES

After deleting specimens with missing characters, I subjected 57 *P. merriami*, 42 *P. m. gilvus*, and 37 *P. flavus* to a stepwise discriminant function analysis using a program (BMD07M) which originated at the Health Sciences Computing Facility, UCLA (Dixon, 1965). I treated the *P. merriami* and *P. flavus* as reference groups, and entered all 42 *P. m. gilvus* as unknowns. A subsequent run using all three as distinct groups yielded substantially similar results.

Explanations and examples of discriminant function analyses are available in Fisher (1936), Morrison (1967), Cooley and Lohnes (1962), and Sokal and Rohlf (1969). Basically, it is a technique for allocating unknown specimens to one of two or more previously recognized groups. It computes a new variable which is a linear function of the original *n* variables that maximizes the distance between the groups. Unknown specimens are scored for the new variable and placed in the most appropriate group.

The analysis is done in stepwise fashion, adding or deleting a single variable at each step. This allows one to determine which characters best separate the groups when used singly or in small combinations. In addition, within groups covariance and correlation matrices are generated, permitting one to determine the degree to which characters are correlated.

The end product is a canonical analysis using all variables (except those which are deleted by the computer). A number of canonical variables equal to the number of characters used in the analysis is extracted. Character coefficients, which may be multiplied by their pooled within group standard deviation to show the contribution of each of the original variables to each of the new canonical variables, are given. In addition, each specimen is assigned a number corresponding to its generalized taxonomic distance (Mahalinobis' distance)

TABLE 3.   Number of individuals classified as *P. merriami* or *P. flavus* after various steps in the discriminant function analysis

	Group	merriami	flavus
Step number 1	*merriami*	53	4
Variables used 1	*flavus*	6	31
	gilvus	35	7
Step number 4	*merriami*	55	2
Variables used 1–4	*flavus*	1	36
	gilvus	33	9
Step number 8	*merriami*	56	1
Variables used 1–8	*flavus*	0	37
	gilvus	27	15
Step number 12	*merriami*	56	1
Variables used 1–12	*flavus*	0	37
	gilvus	25	17
Step number 16	*merriami*	56	1
Variables used 1–16	*flavus*	0	37
	gilvus	24	18
Step number 25	*merriami*	57	0
Variables used 1–23	*flavus*	0	37
	gilvus	27	15

from the mean of each reference group. The probability of a given specimen belonging to a given group is indicated for every specimen in all groups.

Eigenvalues, cummulative proportion of total dispersion, and canonical correlations are calculated for each canonical variable. These values allow one to determine how much of the total available variability is accounted for by each successive canonical variable.

RESULTS

To demonstrate the difficulty encountered in attempting to separate these mice using morphological characters, Figure 4 shows histograms for four of the better characters. These figures clearly show the overlap between *P. merriami* and *P. flavus*, and demonstrate the intermediate nature of *P. m. gilvus*. Table 2 is a list of the original variables in the order the computer entered them into the analysis. Table 3 shows the grouping results of the stepwise analysis at various steps. The characters contributing the most to the first canonical

TABLE 4.   Standardized character coefficients and percent contributions
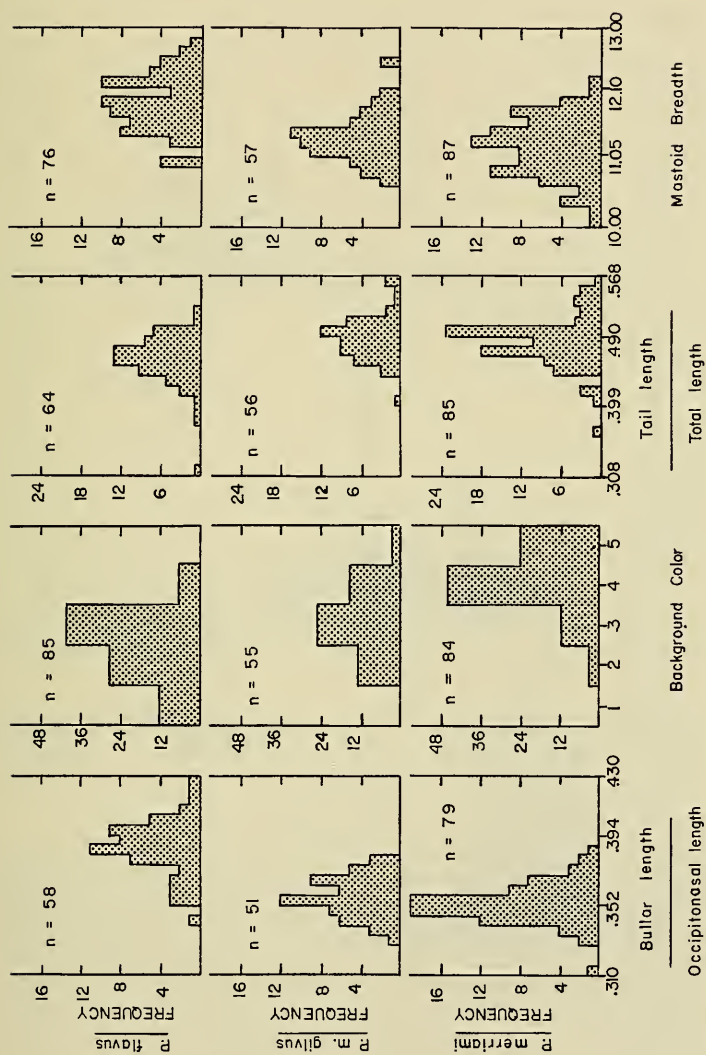to the first canonical variable

	Coefficient	Percent
Occipitonasal length	4.40	11.19
Total length	−3.83	9.74
Interparietal width/Mastoid breadth	3.62	9.21
Bullar length	−3.60	9.16
Interparietal width	−3.56	9.05
Bullar length/Occipitonasal length	3.21	8.16
Hind foot length/Total length	−3.07	7.81
Nasal length	−2.71	6.89
Hind foot length	2.50	6.36
Tail length/Total length	−2.03	5.16
Tail length	1.83	4.65
Mastoid breadth	1.28	3.26
Nasal length/Occipitonasal length	1.00	2.54
Mastoid breadth/Occipitonasal length	0.45	1.14
Lateral line	−0.42	1.07
Background color	−0.39	0.99
Postauricular patch	0.32	0.81
Dorsal black	−0.31	0.79
Interparietal length	0.26	0.66
Frontonasal length	0.24	0.61
Maxillary toothrow length	0.22	0.56
Silkiness	−0.04	0.10
Interorbital constriction	−0.03	0.08

variable are not the same as those at the top of the list. Table 4 gives the standardized coefficients and the percentage contribution of each of the original variables to the first canonical variable.

Histograms of the discriminant scores of the first canonical variable for *P. merriami*, *P. flavus*, and *P. m. gilvus* are presented in Figure 5. It can be seen that although complete separation of *P. merriami* and *P. flavus* can be achieved using multivariate techniques, once again *P. m. gilvus* bridges the gap. Figure 6 is a plot of the first and second canonical

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FIG. 4.   Histograms showing single character separation for four of the best characters. *Perognathus flavus* on top, *P. m. gilvus* in the middle, and *P. merriami* on the bottom.
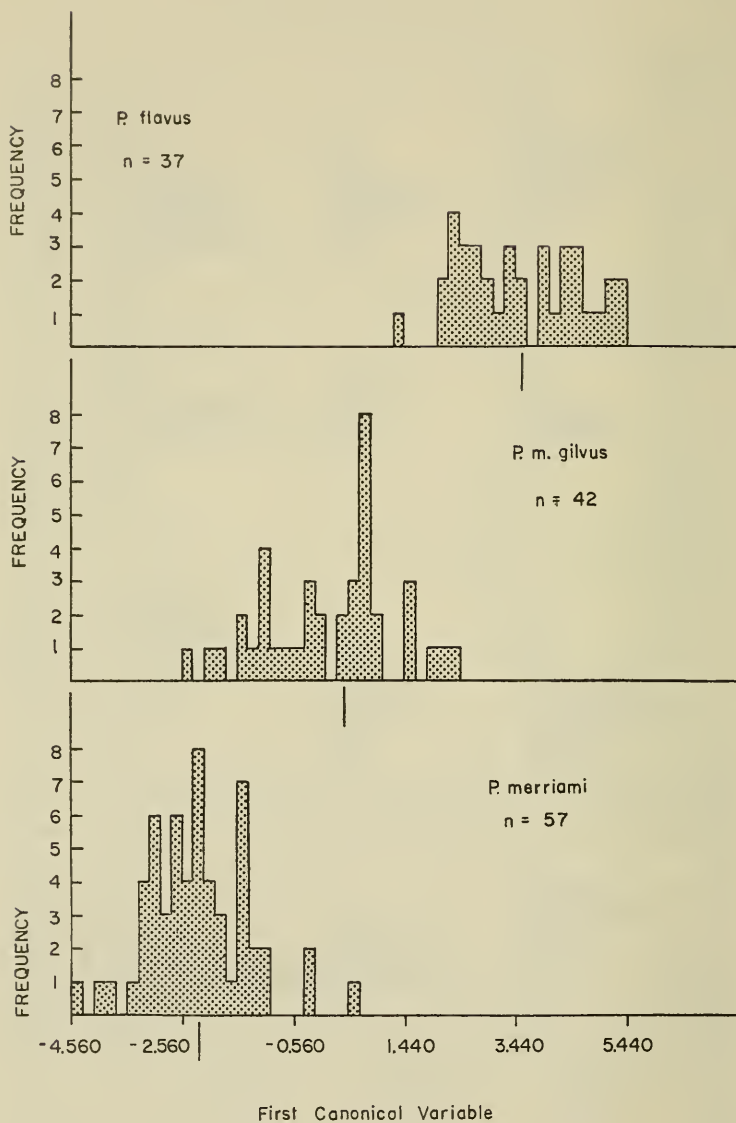
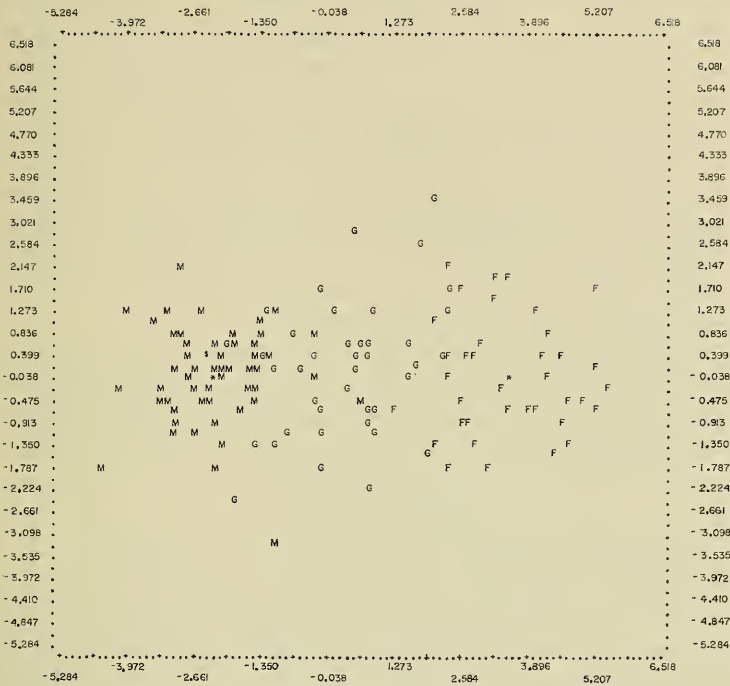Fig. 5. Histograms showing distribution of the first canonical variable.

Fig. 6. Plot of the first and second canonical variables. m = *P. merriami*, g = *P. m. gilvus*, f = *P. flavus*, * = group means, $ = overlap.

variables, and includes all of the specimens used in the analyses.

Discussion

Table 2 and Figure 4 both illustrate the difficulties which faced taxonomists working with these animals in the past. Although differences can be seen between certain individuals, quantifying those differences and finding characters which are useful in allocating all individuals is extremely difficult. Table 3 shows that the best single character, Bullar length/Occipito-nasal length, is not sufficient to allocate all of the individuals correctly. Using this character, four of the *P. merriami* and six of the *P. flavus* are incorrectly allocated, while 35 of the *P. m. gilvus* are allocated to *P. merriami* and seven to *P. flavus*.

Using the four characters shown in Table 2 in combination, only two *P. merriami* and one *P. flavus* are misallocated, and two additional *P. m. gilvus* are switched to *P. flavus*. All of the *P. flavus* and all but one of the *P. merriami* are correctly allocated using eight characters. At this step, 27 *P. m. gilvus* are assigned to *P. merriami* and 15 to *P. flavus*. This is the same as the final proportions for *P. m. gilvus*. At 16 and 20 characters, the proportion of *P. m. gilvus* allocated to *P. flavus* continues upward through 17 to 18. The final step correctly allocates all of the reference samples, and places 27 *P. m. gilvus* in *P. merriami* and 15 in *P. flavus*.

Of the reference *P. merriami* sample, one had a probability of 0.953 and one of 0.999 of being in the right group, and all of the rest were 1.000. For *P. flavus*, there were 2 with 0.953, 1 with 0.993, 1 with 0.998, 2 with 0.999 and the rest were 1.000. The 27 *P. m. gilvus* allocated to *P. merriami* had probabilities ranging from 0.953 to 1.000. Three *P. m. gilvus* had probabilities of 0.500 for both groups.

The three intermediate specimens included one from 25 mi. W of Tucumcari, New Mexico, one from Comstock, Texas, and one from near Kermit, Texas. Osgood (1900) considered the Comstock specimen to be an intermediate between typical *P. merriami* and *P. m. gilvus*. The type-specimen of *P. m. gilvus* was allocated to *P. flavus* with a probability of 0.731.

The cumulative proportions of total dispersion for the first two canonical variables were 0.99861 and 0.99971, respectively, and corresponding eigenvalues were 8.21030 and 0.00906. This indicates that the data illustrated in Figures 5 and 6 account for virtually all of the variability within these samples.

Figure 6 probably illustrates quite well the actual relationships between these three groups. *Perognathus m. gilvus* is a geographically intermediate population between *P. flavus* to the west and *P. merriami* to the east. I suggest that the overlap shown in Figure 6 is probably indicative of the population now known as *P. m. gilvus* interbreeding with *P. flavus* in Eastern New Mexico and Western Texas, and with *P. merriami* in south-central Texas. Data are at present insufficient to determine whether the zone of overlap between *P. flavus* and *P. m. gilvus* is a narrow one limited to Eastern

New Mexico and adjacent portions of Western Texas or whether the integration is more broadly clinal over the whole range of *P. m. gilvus.*

Throughout this analysis, *P. m. gilvus* has been demonstrated to be closer to *P. merriami* than to *P. flavus.* This is not surprising, since the majority of the specimens are from areas that are geographically closer to *P. merriami* than to *P. flavus.* This probably also explains the early allocations of this population to *P. merriami,* rather than to *P. flavus,* even though the close relationships of all three were noted (Osgood, 1900).

In conclusion then, it seems best to regard *P. flavus* and *P. merriami* as conspecific. The three populations are certainly distinct enough to retain subspecific status with the easternmost population known as *Perognathus flavus merriami,* and the intermediate population as *Perognathus flavus gilvus.*

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